

# Dietary Habits of *Solenopsis invicta* (Hymenoptera: Formicidae) in Four Oklahoma Habitats

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**ABSTRACT** Dietary habits of the red imported fire ant, *Solenopsis invicta* Buren, were investigated in four southern Oklahoma habitats: lakeshore, mixed grassland, wooded roadside, and unimproved pasture. Vegetation characteristics of each site were recorded for spring and late summer, in conjunction with estimates of forager success (the percentage of foragers returning to colonies with solid particles or liquid loads). Foragers collected a wide variety of solid particles, with different arthropod prey dominating samples within different sites. At the lakeshore site (no vegetation), dipteran adults, larvae, and pupae comprised >58% of foraged particles. Isoptera comprised >21% of foraged particles at the wooded roadside site. At grassland and pasture sites, seeds (17.2 and 15.7%, respectively) were important foraged items. Forager success rates were highest for solids at the lakeshore site ( $\approx 30\%$  and  $16\%$  in spring and late summer, respectively), and highest for liquids at the pasture site ( $\approx 30\%$  and  $22\%$  for spring and late summer, respectively). Possible influence of vegetation on success rates, and implications for estimates of foraging energetics, are discussed.

**KEY WORDS** *Solenopsis invicta*, diet, foraging, liquid food, solid food, success rates

THE RED IMPORTED fire ant, *Solenopsis invicta* Buren, was accidentally introduced into the United States in Mobile, AL, in the 1930s. Fire ants (*Solenopsis* spp.) are often referred to as "lard ants" or "grease ants" because of their attraction to oily or greasy food sources (Trager 1991). *S. invicta* are aggressive, generalist predators (Wilson and Oliver 1969, Lofgren et al. 1975), are also considered serious seed predators (Drees et al. 1991, Ready and Vinson 1995), and tend homopterans for honeydew (Hays and Hays 1959, Kaakeh and Dutcher 1992, Michaud 1998).

The impact of *S. invicta* in different environments can vary according to its foraging behavior. In Louisiana sugarcane, for example, *S. invicta* is an important natural enemy of the sugarcane borer, *Diatraea saccharalis* Fab. (Reagan 1986). In cotton, *S. invicta* preys on such important pests as beet armyworm, *Spodoptera exigua* Hübner (Ruberson et al. 1994) and corn earworm, *Helioverpa zea* (Boddie). *S. invicta* also preys on medically important arthropods, such as ticks (Harris and Burns 1972). Alternatively, *S. invicta* can directly damage crops and possibly native plants by tunneling in roots, as in cucumber and sunflower (Stewart and Vinson 1991), or indirectly, by protect-

ing plant pests such as aphids (Vinson and Scarborough 1989, Michaud and Browning 1999). Overall effects of *S. invicta* on native vegetation and arthropod communities remain poorly understood. As multiple-queen (polygyne) fire ants move into new areas, arthropod communities in those areas may change drastically, resulting in reduced ant diversity and changes in abundance of ground-dwelling arthropods (Porter et al. 1988, Porter and Savignano 1990).

Green (1952) investigated foraging habits of *S. invicta* in Mississippi, finding that foragers attacked and killed several species of insects, and collected bits of insects. Hays and Hays (1959) recorded a number of foraged items for *S. invicta* in Alabama, including "fly larvae," aphids, small spiders, and some beetles. Foragers killed live insects and collected fragments of dead insects. Wilson and Oliver (1969) conducted a more detailed analysis of prey items collected by foraging *S. invicta* in pine forest and pasture habitats of southeastern Louisiana. In pastures, collembola were the most common prey item, while in pine forests termites made up the largest percentage of foraged material. Foragers were more likely to collect smaller, less mobile insects, and larval forms were collected more frequently than adults. Tennant and Porter (1991) found that foraging *S. invicta* in Texas collected liquid foods more frequently than solid foods, and identifiable fragments collected by *S. invicta* and a native fire ant species exhibited a 59% overlap. Ali et

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al. (1984) manipulated vegetation in Louisiana sugarcane and demonstrated differences in probability of interspecific encounter and foraging efficiency of *S. invicta* in grass, broadleaf, and weed-free habitats. They also observed *S. invicta* foraging on pollen and nectar in broadleaf habitats, where plants were in bloom, and noted decreased foraging efficiency for insect prey where these additional resources were available.

Nothing has been reported on the dietary habits of *S. invicta* in Oklahoma. Infested areas in Oklahoma represent some of the northernmost infestations in the United States, and likely contain a somewhat different suite of available prey items than more southern areas where previous research has taken place. Knowledge of foraged items might lead to prediction of impacts on arthropod communities as new areas in Oklahoma are invaded. Information on forager success rates might have implications for control success with bait products, and would be very useful for the construction of foraging energy budgets. Tennant and Porter (1991) hypothesized that exploitation of liquid food sources might explain how *S. invicta* is able to maintain extremely dense field populations. This might be especially relevant in southern Oklahoma, where the percentage of the year suitable for foraging is less than the percentage in other areas where similar dietary studies have been pursued (e.g., southcentral Texas, southern Louisiana) (J.T.V., unpublished data). For these reasons, we undertook a study to characterize forager success rates and dietary habits of *S. invicta* in four Oklahoma habitats: unimproved pasture, wooded roadside, undisturbed grassland, and lakeshore. Lakeshore habitats were of particular interest, considering frequent complaints of fire ants interfering with fishing and other recreational activities in these areas. Secondary objectives of this research were to determine whether ants were attracted to lakeshore habitats for water or for prey items, and to examine the relative importance of liquid and solid foods at the study sites. Possible relationships between vegetation and forager success are discussed.

### Materials and Methods

**Study Sites.** Four sites, representing common southern Oklahoma habitats, were identified for this study in spring 1999. Pasture and wooded roadside sites were located near Milburn, Johnston County, OK (34° 08' 35' N, 96° 30' 09' W) (pasture and roadside, respectively). Grassland and shoreline sites were located at Lakeside Recreational Area near Platter, OK (on Lake Texoma) (33° 56' 15' N, 96° 33' 02' W) (lakeside and lakeshore, respectively). Vegetation was sampled at each site in spring 2000 and again in late summer 2000. Two 30-m transects were established at each site, and a 900-cm<sup>2</sup> quadrat was employed to sample six subplots along each transect. Diversity indices were obtained by noting presence of each plant species occurring within each subplot. Biomass was determined by clipping and gathering all standing vegetation in each subplot, drying at 50°C for 48 h, and weighing

material to the nearest 0.1 g. All standing plant material, living and dead, was collected.

**Dietary Habits.** Colonies at the pasture, grassland, and wooded roadside sites were prepared for sampling by digging a shallow trench (≈5 cm deep by 10 cm wide) around each mound to be sampled, and allowing foraging ants 30 min to 1 h to reconnect their foraging trails across the bottom of the trench. Foraged material was obtained by closely observing foragers returning to mounds, and collecting those that appeared to be carrying solid particles, either with forceps or an aspirator. Foragers tend to hold onto foraged material even when collected with forceps (Tennant and Porter 1991). At the lakeshore site, foraging trails from colonies in tall grass on the shore extended across barren sand to the water's edge. These were easily detected by the presence of loose sand on the surface directly above the trails. To collect material at this site, trails were exposed with a trowel and collection proceeded as above.

*Solenopsis invicta* commonly deposit dead nestmates and other debris in discrete piles around their nests (referred to as "refuse piles" herein). To further describe dietary habits of the ants, five large (>3 cm diameter) refuse piles were collected from each study site (20 total) and sorted for identifiable insect remains. Collections took place in spring 1999.

**Forager Success.** Forager success rates were determined using timed observations of foragers moving along trails in the direction of a colony. Success rates were calculated as the percent of incoming foragers carrying solid particles or liquid loads. Liquid-bearing foragers can be identified by the striped appearance of the abdomen, resulting from exposure of the intersegmental membrane when the crop is expanded (Tennant and Porter 1991). Estimates were timed to coincide with vegetation measurements (spring and late summer) at the study sites. Mean soil temperature (2 cm deep) and ambient temperature in shade were recorded before sampling. The number of trails observed varied according to the number of active trails exposed during sampling (range, 7–20). To determine predictive value of vegetation indices on success rates, data (percent of foragers carrying liquids, percent of foragers carrying solids) were subjected to Proc MIXED (Littell et al. 1996) with date (site) as a random effect, and site and vegetation indices as fixed effects. An examination of type 1 and type 3 *F* values for site was used to determine the increase in precision from adding each vegetation index to the model. Finally, site was used as a blocking factor in an analysis of variance (ANOVA) (PROC GLM) (SAS Institute 1985) to determine temperature effects on success rates, as well as for comparing solid v. liquid success.

### Results

**Site Characteristics.** In general, vegetation at pasture and lakeside sites consisted of low growing herbaceous plants. The roadside site also contained a dense (≈462 trees ha<sup>-1</sup>) stand of trees (primarily hackberry, *Celtis laevigata* Willdenow.) with moder-

Table 1. Vegetation characteristics at three southern Oklahoma study sites

Site	Dominant species <sup>a</sup>		(B) Biomass <sup>b</sup> (C) Dominance <sup>c</sup> (H') Equitability <sup>d</sup> (N) Species Richness <sup>e</sup>
	Spring	Summer	Spring      Summer
Lakeside	Forbs:	Forbs:	
	<i>Erigeron</i> sp. (fleabane) (0.08)	<i>Lespedeza</i> sp. (0.18)	B: 6 ± 1b      23 ± 5a
	<i>Medicago</i> sp. (alfalfa) (0.08)	<i>Cassia</i> sp. (0.16)	
	<i>Lespedeza</i> sp. (0.07)	<i>Phylla</i> sp. (fogfruit) (0.14)	C: 0.067      0.127
	Grasses:		
Pasture	<i>Bromus</i> sp. (0.07)		H': 1.123      0.317
	<i>B. japonicus</i> Thunb. (Japanese brome) (0.07)		N: 19      13
	<i>Panicum</i> sp. (0.07)		
	Forbs:	Forbs:	
	<i>Medicago</i> sp. (alfalfa) (0.13)	<i>Ambrosia artemesiifolia</i> L. (little ragweed) (0.38)	B: 17 ± 2a      21 ± 3a
Roadside	<i>Ambrosia artemesiifolia</i> L. (little ragweed) (0.10)		C: 0.083      0.303
	<i>Stellaria</i> sp. (chickweed) (0.08)	Grasses:	
	<i>Oenothera</i> sp. (evening primrose) (0.08)	<i>Aristida</i> sp. (0.27)	H': 1.166      0.590
	Grasses:	<i>Eragrostis</i> sp. (0.15)	
	<i>Agrostis</i> sp. (0.12)	Unknown (0.15)	N: 17      5
	<i>Bromus</i> sp. (0.07)		
	Forbs:	Unknown sedge (0.16)	
	<i>Triodanis</i> sp. (0.13)	Unknown grass (0.16)	B: 6 ± 1b      17 ± 1a
	<i>Osmorhiza</i> sp. (sweet cicely) (0.12)		
	<i>Galium</i> sp. (bedstraw) Trees <sup>f</sup> (0.12)		C: 0.098      0.114
	<i>Celtis laevigata</i> Willd. (hackberry) (0.74)		H': 1.102      0.995
	<i>Ulmus crassifolia</i> Nutt. (cedar elm) (0.19)		
	<i>Maclura pomifera</i> (Raf.)		N: 18      3
	Schneid. (osage orange) (0.07)		

<sup>a</sup> Name (common name) (proportion). Only most abundant species reported.  
<sup>b</sup> Mean g/900 cm<sup>2</sup> ± SE. Means in the same column followed by the same letter are not significantly different (ANOVA, P > 0.05).  
<sup>c</sup> Simpson index  $C = \frac{\sum_{i=1}^s p_i^2}{\sum_{i=1}^s p_i^2}$  where  $p_i$  is the proportion of each of  $s$  species.  
<sup>d</sup> Shannon-Wiener index  $H' = -\sum_{i=1}^s p_i \log p_i$  where  $p_i$  is the proportion of each of  $s$  species.  
<sup>e</sup> Number herbaceous species encountered.  
<sup>f</sup> Trees considered separately from other plants, and sampled only in spring; name (common name) (importance value).

ate undergrowth. Vegetation sampling was not done at the lakeshore site, where the sampling area consisted of barren sand (with the exception of dead and decaying plant material in the debris line along the water's edge). Vegetation characteristics are summarized in Table 1. Herbaceous species richness and equitability declined and dominance increased at all sites from spring to late summer. Above-ground biomass increased at the lakeside and roadside sites from spring to late summer (Table 1); much of this increase was due to dead but standing vegetation from earlier spring growth.

**Foraged Material.** *S. invicta* foraged on a variety of materials in each habitat (Table 2). A large percentage of material recovered during this study was not identifiable (range, 10.2–46.8%). Animal material made up the bulk of collections; however, seeds were an important component of foraged material at the lakeside (17.2%) and pasture (15.7%) study sites. A small percentage (<5%) of unidentified particles appeared to be of plant origin; these were not counted separately. Foraging continued even when drought destroyed nearly all the understory vegetation at the roadside site.

The dominant foraged items at the lakeshore study site were partial and whole dipterans (58.5%), both larvae and adults. *S. invicta* foragers could be seen on the ground surface foraging in the debris line at the water's edge. Collembolans were also abundant in lakeshore collections (23.3%). Damsel bugs made up a small (1.1%) portion of the foraged items. These generalist predators may have been attracted to the lakeshore to feed on nematocerans, although their feeding activity was not observed. At the lakeside site, seeds (17.2%) were followed in abundance by collembolans (11.6%). Homopterans (7.5%) and spiders (6.7%) were also collected frequently. At the roadside site, termites (21.7%) and isopods (7.5%) were abundant. Fragments of isopod exoskeleton were commonly seen on and around mounds in the roadside habitat. In the pasture, seeds (15.7%), homopterans (7.6%), and collembolans (6.6%) were most abundant.

**Contents of Refuse Piles.** Whole and partial remains of coleopterans made up the bulk of material retrieved from refuse piles (Table 3), with the exception of dead *S. invicta* workers (not counted) and one refuse pile in which aphids were especially abundant. The number of identifiable fragments recovered from refuse

Table 2. Identification of particles foraged by *S. invicta* in 4 Oklahoma habitats

Foraged item	Lakeshore		Lakeside		Roadside		Pasture	
	No. of items	% of total	No. of items	% of total	No. of items	% of total	No. of items	% of total
Collembola	190	23.3	31	11.6	9	1.3	43	6.6
Diptera (total)	477	58.5	8	3.0	25	3.5	19	2.9
Adults (unknown)	7		2		6		8	
Pupae (unknown)	16		0		2		5	
Larvae (unknown)	0		0		3		2	
Nematocera larvae	43		0		8		0	
Nematocera adults	383		3		4		4	
Brachycera larvae	28		0		1		0	
Cyclorrhapha larvae	0		1		0		0	
Muscidae adults	0		2		0		0	
Coleoptera (total)	8	1.0	9	3.4	27	3.8	32	4.9
Adults (unknown)	4		3		9		10	
Larvae (unknown)	1		3		13		7	
Pupae (unknown)	1		2		0		0	
Ptiliidae	1		0		0		0	
Carabidae	0		0		0		1	
Carabidae larvae	0		0		1		10	
Chrysomelidae	1		0		3		2	
Anthocoridae	0		0		1		1	
Erotylidae	0		1		0		0	
Coccinellidae larvae	0		0		0		1	
Orthoptera	0	0	2	0.7	7	1.0	27	4.2
Araneae	6	0.7	18	6.7	9	1.3	36	5.5
Hymenoptera (total)	1	0.1	10	3.7	5	0.7	9	1.4
Formicidae	1		1		3		8	
Formicidae pupae	0		7		0		0	
Acari	0	0	4	1.5	16	2.3	7	1.1
Homoptera (total)	0	0	20	7.5	34	4.8	49	7.6
Cicadellidae	0		11		20		42	
Coccoidea	0		0		1		2	
Aphididae	0		6		2		1	
Membracidae	0		0		1		0	
Lepidoptera larvae	0	0	7	2.6	4	0.6	9	1.4
Hemiptera (total)	14	1.7	5	1.9	5	0.7	12	1.8
Nabidae	9		0		0		0	
Lygaeidae	2		0		0		2	
Thyreororidae	0		0		1		0	
Miridae	1		0		0		0	
Cixiidae	0		1		0		0	
Pentatomidae	0		0		0		3	
Isoptera	0	0	0	0	154	21.7	0	
Isopoda	0	0	1	0.4	53	7.5	0	
Diplopoda	0	0	0	0	8	1.1	0	
Chilopoda	0	0	3	1.1	3	0.4	0	
Psocoptera	3	0.4	0	0	1	0.1	0	
Thysanoptera	3	0.4	2	0.7	4	0.6	0	
Unidentifiable items	83	10.2	102	38.1	305	42.9	304	46.8
seeds	31	3.8	46	17.2	42	5.9	102	15.7
Total	816		268		711		649	

piles was highly variable, ranging from 442 (lakeside) to one (pasture). Mean number of particles per refuse pile was highly variable, and not different between sites (ANOVA;  $P = 0.2$ ) (Table 3).

**Forager Success Rates.** Vegetation changes seasonally and is both a direct (availability of nectar, pollen, and plant sap) and indirect (availability of associated insects) measure of resource availability. A model (liquid success = site + vegetation index) combining species richness (N) and site as fixed effects best described liquid success rates (for site,  $F = 7.7$ ;  $df = 2, 11$ ;  $P = 0.008$  and for N,  $F = 6.2$ ;  $df = 1, 11$ ;  $P = 0.03$ ); adding N to the model increased the type 3  $F$  for site by  $\approx 32\%$ . Liquid food retrieval dropped as species richness decreased. Solid food retrieval was related to site ( $F = 5.4$ ;  $df = 2,$

$11$ ;  $P = 0.02$ ); however, adding vegetation indices to the model did not result in any increase in precision.

Neither ambient nor soil temperature had any significant effect on success rates or overall ant activity ( $P > 0.05$ ; GLM blocked by site, data square root-transformed). Sampling was performed within a reasonably wide range of temperatures ( $18.3\text{--}34.5^\circ\text{C}$  at 2 cm soil depth); however,  $>75\%$  of samples were taken when soil temperatures were between  $25$  and  $33^\circ\text{C}$  to maximize collection of foraged particles.

At the lakeshore site, the percent of successful foragers returning with solids was  $\approx 86\%$  greater in spring than in summer (GLM) ( $F = 12.4$ ;  $df = 1, 16$ ;  $P = 0.003$ ); collection of solids was consistent between seasons at other sites ( $P > 0.05$ ). At the roadside site,

**Table 3.** Identification of arthropod remains recovered from refuse piles of *S. invicta* in four Oklahoma habitats

Site	Identification	No. of fragments	Mean no. fragments per refuse pile <sup>a</sup>
Lakeshore	Coleoptera (total)	144	57 ± 14
	Chrysomelidae	2	
	Curculionidae	11	
	Carabidae	27	
	Scarabeidae	2	
	Elateridae (larva)	1	
	Anthicidae	3	
	Bostrichidae	1	
	Homoptera (total)	40	
	Aphididae	39	
	Cicadellidae	1	
	Hemiptera (total)	7	
	Hymenoptera (total)	5	
	Halictidae	1	
	Parasitoid (unknown)	1	
	Araneae	1	
Lakeside	Coleoptera (total)	95	117 ± 82
	Curculionidae	10	
	Carabidae	6	
	Scarabeidae	32	
	<i>Martinezia dutertrei</i> (Chalumeau)	25	
	Anthicidae	2	
	Staphylinidae	1	
	Tenebrionidae	1	
	Homoptera (total)	196	
	Aphididae	195	
	Cicadellidae	1	
	Hemiptera (total)	10	
	Thyreocoridae	2	
	Hymenoptera (total)	3	
	Parasitoid (unknown)	1	
Pasture	Coleoptera (total)	7	5 ± 1
	Carabidae	2	
	Scarabeidae	1	
	Homoptera (total)	4	
	Aphididae	4	
	Acari	1	
	Collembola	2	
	Diptera (Nematoceran larva)	2	
Roadside	Coleoptera (total)	11	7 ± 1
	Curculionidae	3	
	Scarabeidae	1	
	<i>Martinezia dutertrei</i> (Chalumeau)	1	
	Homoptera	1	
	Acari	1	

<sup>a</sup> Mean ± SE.

liquid success rates were  $\approx 77\%$  higher in spring than in summer (GLM) ( $F = 15.6$ ;  $df = 1, 23$ ;  $P = 0.0007$ ) but statistically indistinguishable at other sites. Success rates are presented graphically in Fig. 1.

### Discussion

Solid particles collected by *S. invicta* workers in Oklahoma habitats were similar to particles collected and identified in other studies (e.g., Hays and Hays 1959, Wilson and Oliver 1969, Tennant and Porter 1991). Red imported fire ants are truly omnivores, as evidenced by the broad range of arthropods and seeds they prey on and their ability to thrive in different habitats. As in Louisiana (Wilson and Oliver 1969), *S.*

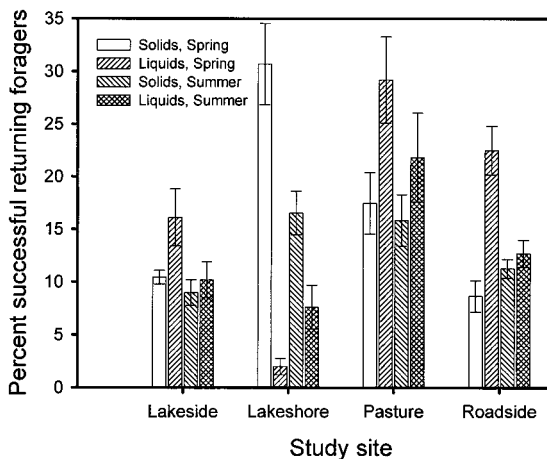


Fig. 1. Success rates (percent of foragers with solid or liquid food) of incoming *S. invicta* foragers in four Oklahoma habitats.

*invicta* in Oklahoma prey on termites in wooded habitats (Roadside). One interesting exception to other published accounts was the abundance of seeds in foraged material, particularly at the lakeside (17.2%) and pasture (15.7%) sites. Wilson and Oliver (1969) reported that seeds made up  $\approx 1.5\%$  of the diet of *S. invicta*; Tennant and Porter (1991) reported 3.9%. *S. invicta* colonies do not possess a specialized caste for handling and crushing seeds; however, in southern Oklahoma they are occasionally reported to cause stand loss in wheat due to their feeding activities (W. A. Smith, personal communication). *S. invicta* can cause damage to a variety of crop seeds, especially seeds that have imbibed water (Morrison et al. 1999), and feed preferentially on some wildflower seeds (J.T.V., A. Armstrong, and S.A.R., unpublished data). High rates of seed predation in this study warrant further investigation into possible effects of *S. invicta* on distribution and abundance of native vegetation.

Not surprisingly, refuse piles contained many fragments and whole specimens of highly-sclerotized coleopterans (Table 3). Interestingly, at the lakeshore and lakeside sites, aphids were relatively abundant in refuse piles. It is not known whether the aphids were parasitized, died naturally while being tended, or served as prey for the ants. One might suspect that because aphids are soft-bodied, they would easily be torn apart and fed to fourth-instar larvae within the colony. Further investigation of refuse piles and their contents is necessary to explain the phenomenon of large numbers of aphids in some piles.

One notable coleopteran collected from refuse piles at the lakeside and roadside sites was *Martinezia dutertrei* (Chalumeau), a myrmecophile that obtains food from live ants, larvae, and dead worker corpses (Wojcik et al. 1991). It is not known why this species was collected at the lakeside site and not the lakeshore site, because only a few hundred meters separated them. Live *M. dutertrei* were observed around *S. invicta* mounds at the lakeside site, usually in association



with refuse piles (burrowed partially into the soil underneath the piles); at times, we observed 15 or more of these beetles around single mounds where ants had piled debris in previously-used trenches.

With the exception of the lakeshore study site, which was essentially devoid of vegetation, liquid success rates were numerically greater in spring than in late summer (Fig. 1). Possible sources of liquid exploited by ants include plant nectar (from reproductive, floral, and extrafloral nectaries), honeydew-producing homopterans, and hemolymph of prey insects. Tennant and Porter (1991) analyzed crop contents of *S. invicta*, and determined that plant sap, plant nectars, and homopteran honeydew were more likely sources than insect hemolymph. The decline in species richness of plants within study sites from spring to late summer might account for the decline in liquid success rates, both directly (by affecting availability of nectar) and indirectly (by affecting population densities of honeydew-producing homoptera). Direct comparison of forager success rates among habitats is difficult because forager success appears to be resource-dependant (e.g., Ali et al. 1984) and prey and liquid food sources were not quantified in our study; however, species richness appears to have some possible value for modeling liquid success. A more thorough examination of success rates, incorporating more sampling dates, would be useful for testing these relationships. Forbs likely provide more resources in the form of plant sap, nectar, and homopteran populations than grasses. Drought during the summer of 2000 may have affected both plant communities and ant activity at our sites.

Changes in forager success rates could have marked effects on colony energetics and foraging energy budgets. Dramatic changes in solid collection (e.g., lakeshore site) and liquid collection (e.g., roadside site) could change foraging energetics on a seasonal basis, and the differences in success rates between sites indicate varying returns for foraging activity for fire ant populations in different areas. Construction of energy budgets for *S. invicta* will have to take these differences into account to yield reasonable estimates that can be applied to populations across seasons and locations. Differences between habitats may also have implications for competitive interactions between ant species. As Tennant and Porter (1991) noted regarding displacement of the tropical fire ant [*S. geminata* (F.)] by *S. invicta*, differences in foraging efficiency between species in one habitat should be studied in different habitats. Obviously, some habitats yield a greater abundance of prey to sustain colonies, while some yield a greater amount of liquid food available to foragers. Other ant species were occasionally noted in the pasture habitat during this study (*Monomorium* sp. and *Forelius* sp.), but not at the other sites.

It is evident from relatively low liquid success rates ( $\approx 3\text{--}8\%$ ) that foragers at the lakeshore site were not attracted to that area primarily in search of water, though no attempt was made to characterize the liquid in their crops. The lack of vegetation and associated homopterans at this site may have reduced liquid suc-

cess rates. Lakeshore data presented herein are not appropriate for estimating foraging energetics because they reflect foraging habits in only part of the habitat surrounding the colonies. These data reveal, however, the ability of *S. invicta* to exhibit high success rates for solid food particles ( $>30\%$ ), and exploit abundant resources within its environment.

In conclusion, *S. invicta* foraged on a wide variety of solid particles—many similar to previous studies. In the lakeshore habitat, foragers appeared to efficiently exploit a specific, abundant resource. *S. invicta* exhibits different success rates for solid and liquid food in different Oklahoma habitats. Although not tested directly, differences in liquid food collection appear to be related to differences in vegetation and/or associated Homoptera.

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### References Cited

- Ali, A. D., T. E. Reagan, and J. L. Flynn. 1984. Influence of selected weedy and weed-free sugarcane habitats on diet composition and foraging activity of the imported fire ant (Hymenoptera: Formicidae). *Environ. Entomol.* 13: 1037–1041.
- Drees, B. M., L. A. Berger, R. Cavazos, and S. B. Vinson. 1991. Factors affecting sorghum and corn seed predation by foraging red imported fire ants (Hymenoptera: Formicidae). *J. Econ. Entomol.* 84: 285–289.
- Green, H. B. 1952. Biology and control of the imported fire ant in Mississippi. *J. Econ. Entomol.* 45: 593–597.
- Harris, W. G., and E. C. Burns. 1972. Predation on the lone star tick by the imported fire ant. *Environ. Entomol.* 1: 362–365.
- Hays, S. B., and K. L. Hays. 1959. Food habits of *Solenopsis saevissima richteri* Forel. *J. Econ. Entomol.* 52: 455–457.
- Kaakeh, W., and J. D. Dutcher. 1992. Foraging preference of red imported fire ants (Hymenoptera: Formicidae) among three species of summer cover crops and their extracts. *J. Econ. Entomol.* 85: 389–394.
- Littell, R. C., G. A. Milliken, W. R. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.
- Lofgren, C. S., W. A. Banks, and B. M. Glancey. 1975. Biology and control of imported fire ants. *Annu. Rev. Entomol.* 20: 1–30.
- Michaud, J. P. 1998. A review of the literature on *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Fla. Entomol.* 81: 37–61.
- Michaud, J. P., and H. W. Browning. 1999. Seasonal abundance of the brown citrus aphid, *Toxoptera citricida*, (Ho-

- moptera: Aphididae) and its natural enemies in Puerto Rico. *Fla. Entomol.* 82: 424–447.
- Morrison, J. E., D. F. Williams, D. F., and D. H. Oi. 1999. Effect of crop seed water content on the rate of seed damage by red imported fire ants (Hymenoptera: Formicidae). *J. Econ. Entomol.* 92: 215–219.
- Porter, S. D., B. Van Eimeren, and L. E. Gilbert. 1988. Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography of competitive replacement. *Ann. Entomol. Soc. Am.* 81: 913–918.
- Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106.
- Ready, C. C., and S. B. Vinson. 1995. Seed selection by the red imported fire ant (Hymenoptera: Formicidae) in the laboratory. *J. Econ. Entomol.* 24: 1422–1431.
- Reagan, T. E. 1986. Beneficial aspects of the imported fire ant: a field ecology approach, pp. 58–71. In C. S. Lofgren and R. K. Vander Meer [eds.], *Fire ants and leafcutting ants: biology and management*. Westview, Boulder, CO.
- Ruberson, J. R., G. A. Herzog, W. R. Lambert, and W. J. Lewis. 1994. Management of the beet armyworm (Lepidoptera: Noctuidae) in cotton: role of natural enemies. *Fla. Entomol.* 77: 440–454.
- SAS Institute. 1985. SAS user's guide: statistics, version 5th ed. SAS Institute, Cary, NC.
- Stewart, J. W., and S. B. Vinson. 1991. Red imported fire ant damage to commercial cucumber and sunflower plants. *Southwest. Entomol.* 16: 168–170.
- Tennant, L. E., and S. D. Porter. 1991. Comparison of the diets of two fire ant species (Hymenoptera: Formicidae): Solid and liquid components. *J. Entomol. Sci.* 26: 450–465.
- Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *J. N.Y. Entomol. Soc.* 99: 141–198.
- Vinson, S. B., and T. A. Scarborough. 1989. Impact of the imported fire ant on laboratory populations of cotton aphid (*Aphis gossypii*) predators. *Fla. Entomol.* 72: 107–111.
- Wilson, N. L., and A. D. Oliver. 1969. Food habits of the imported fire ant in pasture and pine forest areas in southeastern Louisiana. *J. Econ. Entomol.* 62: 1268–1271.
- Wojcik, D. P., B. J. Smittle, and H. L. Cromroy. 1991. Fire ant myrmecophiles: Feeding relationships of *Martinezia dutertrei* and *Euparia castanea* (Coleoptera: Scarabaeidae) with their ants hosts, *Solenopsis* spp. (Hymenoptera: Formicidae). *Insectes Soc.* 38: 273–281.

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